LOCOMOTION IN BATRACHOSEPS WITH SEVERED NERVE-CORD.

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The earlier discoveries in the anatomy and physiology of the nervous system led to the conception that the nervous mechanisms of the human body were under the control of a single center, the brain.[1] Discoveries, which have been made in the field of comparative physiology during the past fifty years, however, are lead- to a very different conception.

Not only the spinal cord,[2] but also the brain,[3] is being regarded not as a single nerve-center but as a segmental series of many nerve-centers. Furthermore the idea is gaining ground that true nerve-centers are probably not so greatly differentiated one from the other, — that their respective protoplasmic contents are not so different in nature, as was once supposed. On the other hand it is pointed out that specific differences in the nervous substance is to be looked for in the sense-organs, in the peripheral nerve-substance, rather than in the central organs. Accordingly the central nervous system is to be regarded primarily as a special conduction substance by means of which the sense organs are able to communicate with the various physiological structures in which the efferent nerve-fibers find their termination.[4]

The observations reported in the present paper furnish additional evidence in support of this segmental theory of the central nervous system. In order to make the viewpoint of interpretation of results clearer the work of two other authors will be first briefly reviewed.

Friedländer[5] observed that coördination of the longitudinal

[1] Schiff, "Lehrbuch der Physiologie," 1858, s. 194. Foster, "History of Physiology," 1901, p. 257 ff. Steiner, "Die Functionen des Centralnervensystems und ihre Phylogenese," 2te Abtheilung, Die Fische, 1888, s. 35.

[2] Sherrington in Schaefer's "Text-book of Physiology," p. 816. Loeb, *Arch. f. d. ges. Physiologie*, Bd. 96, s. 536, 1903.

[3] Grünbaum and Sherrington, *Proc. of Roy. Soc.*, Vol. 69, 1901.

[1] Loeb, "Comparative Physiology of the Brain and Comparative Psychology," 1901.

[1] Friedländer, B., "Physiologie des Centralnervensystem," *Arch. f. ges. Physiologie*, Bd. 58, s. 168, 1894.

muscles in earthworms was not disturbed by removal of a small piece of the nerve-cord, that the circular muscles failed to contract only in the region where the cord was removed and that elsewhere they continued to contract rythmically. If the posterior part of such a worm lay on a smooth surface it would allow itself to be dragged along by the part anterior to the section. If, however, the posterior part be dragged over a rough surface, moistened blotting paper for instance, its segments would begin active, rythmical contractions and coöperate with the anterior part in progressive locomotion.

That one part of the body in these worms was not dependent on the nerve-cord of the other part was still better shown in a worm which was cut cross-wise into two halves. The halves were fastened together again by a string. The anterior half, pulling on the posterior half, especially when the latter lay on a rough surface, would produce coördinated movements in the posterior half.

In another experiment only the posterior half was used. It was placed on papers of two grades of roughness, the anterior part on the rougher, the posterior part on the smoother paper. A pull on the rougher paper started up locomotor contractions in the foremost segments; the other segments remained inactive while being dragged over the smooth paper, notwithstanding the fact that the cord was intact in the entire piece of the animal which was under observation.

These phenomena in worms with severed nerve-cords were explained as follows: One segment, shortening, produces a pull on the next segment in the body and thereby stretches the skin of that segment. This stretching process sets up sensory impulses which, passing into their segmental ganglion, are reflected back as motor impulses to muscles of the same segment. The muscle contraction so produced in turn exerts a pull on the skin of the next segment and thereby gives rise to another cycle of sensory-motor impulses, which, as mere nerve-impulses, do not necessarily pass beyond the boundaries of the segment where they originated. And so on, from segment to segment, a motor impulse started at *a* may be transmitted to segments *b*, *c*, *d*, etc., without any impulses whatsoever passing over the fibers in the

nerve-cord which directly connect the ganglia. In short, coördinated locomotion is secured without the nerve cord, as such, coming into play at all. In their passage the nervous impulses involved, according to this conception, do not follow a straight path with side-paths at each segment, but rather follow a path which may best be described as a line of loops.

Friedländer concluded that locomotor movements in the earthworm should not be regarded as the result of a single impulse (say of the anterior segment) which passes through the length of the body, but rather should it be regarded as the result of impulses given off by each segment separately.

2. That coördinated movements in animals higher than worms may be set up and maintained, with the spinal cord brought into use only in spots, as it were, rather than as an entire and single organ, has been recently demonstrated in a remarkable way by the experiments of Phillipson.[1]

It has been known for some time[2] that, if a dog with a sectioned cord be supported so that its hind legs hang freely in space, the legs spontaneously begin an alternate flexor-extensor movement.

Phillipson obtained this so-called pendulum movement of the legs in a dog with sectioned nerve-cord. The movement lasted sometimes for more than an hour; it could be accelerated into a veritable gallop by gently pulling the tail of the animal. The valuable part of this experimenter's work, however, lies in the complete analysis which he was able to make of the various steps involved in the process of locomotion. From his experiments and observations on this dog with the severed nerve-cord, he drew conclusions concerning locomotion in the hind legs of normal dogs somewhat as follows:

The hind-foot of a dog during extension gently comes in contact with the ground; this foot-contact produces a feeble excitation which brings on a flexing of the metatarsals with the sole of the foot supported against the ground. The resistance of the ground against this flexing of the metatarsals produces a sensory-motor wave which brings a sudden halt to all muscular

[1] Phillipson, Maurice, *Comptes Rendus*, Vol. 136, p. 61, 1903.

[2] Freusberg, *Archiv f. die ges. Physiologie*, "Reflex Bewegung beim Hunde.," 1874, Bd. IX., s. 358.

action which in turn throws the body forward. The shock produced by the sudden halt of muscular action causes flexion of the limb which has just reached the limit of extension, and the pulling of the skin at the inguinal region by this same extension, starts up extensor movements in the opposite limb, which in its turn coming in contact with the ground goes through the same cycle of movements just completed in its fellow. And so on, the action of one leg determines that of the other, so that not only walking but running movements in the hind-legs may be, and probably are, kept up indefinitely, involving the use of no more of the nerve-cord than that part in which these simple sensory-motor impulses may be exchanged.

According to Phillipson's analysis it appears quite possible that, *after progressive locomotion has once been started in a normal dog, it might walk or even run a distance without any additional impulses passing down from the upper region of the spinal cord.*

3. The question now arises, *could normal walking movements in the hind legs of an animal be initiated without any impulses whatsoever, for the purpose, coming into the lumbar centers from levels of the cord higher, say, than the mid-dorsal region, or from levels higher than the lumbar region itself.*

Loeb[1] has already suggested that the pendulum movements in the hind-legs of a dog with severed nerve-cord may be caused by the stretching of the skin on the sides of the body produced by holding up the front part of the animal. He further held the opinion that if the beast could stand at all on its legs it probably could go through the coördinate movements necessary for walking. For, if the fore-legs took forward steps that action would produce a pull on the sides of the body, stretching the skin. This stretching would create sensory stimuli that would pass into the lumbar region of the cord whence extensor motor stimuli would pass into one leg or the other and thus start up the cycle of ambulatory motions described by Phillipson. This view of the possibility of coördinating anterior and posterior locomotion in a vertebrate with severed nerve-cord receives strong support from the experiments and observations of Friedländer. But it may be

[1] Loeb, Jacques, "Beiträge zur Gehirnphysiologie der Würmer." *Arch. f. d. ges. Physiologie*, 1894, 56, s. 268.

objected that results obtained from an animal of such pronounced metameric structure as that of the earthworm cannot be applied in the case of vertebrates; that if "the nerve-cord of the earthworm is an apparatus by means of which reflexes may be transferred from one segment to the other"[1] it does not follow that the nerve-cord of a vertebrate in its activity can be reduced to elements equally simple.

In uninjured land animals of the bilateral types progressive locomotion is usually initiated by forward or lateral movements of the anterior part of the body. This action produces an effect on the passive posterior part of the body, especially in the skin, where sensory stimuli may be set up. These sensory stimuli may be aroused in two ways. First, by tugging, the skin is subjected to stretching stimuli; second, by dragging even the slightest distance, the ventral surface of the body, and therefore of the skin of creeping animals, is subjected to a series of rapid, successive impacts against the inequalities of the ground-surface. In other words, by dragging *the skin is subjected to friction stimuli in addition to stretching stimuli.*

Now since the skin is always subjected to more or less such treatment in the initiation of locomotor movements, it is reasonable to suppose that a characteristic combination of sensory stimuli is thereby produced which may be able to set up motor stimuli in centers of corresponding levels. One may suppose moreover that these motor stimuli do not result in vague, purposeless reflexes, but rather that they result in definite, unvarying coördinations; that they are operative and effective without intervening stimuli from other regions of the nerve-cord.

In other words, *a definite combination of sensory stimuli in one region, occasioned by a definite motor activity in another region, may be a sufficient signal for locomotor activity in the region receiving such sensory stimuli.*

4. At the suggestion of Dr. Loeb, for whose constant assistance and kindly interest in my work I wish here to express my best thanks, I began some experiments during February of this year to test the truth of the ideas set forth in the foregoing paragraphs.

[1] Freidländer, *loc. cit.*, p. 206.

The animal selected for experimentation was *Batrachoseps*. This is a small batrachian with a long, slender body and ridiculously short, slender legs which, while perfectly functional, are not depended upon to carry on all the work of locomotion. The complete musculature of the body-walls and of the long, slender tail is evidence that they, too, at times assist mightily in locomotion. Indeed in the normal animal one sees that for leisurely movements only the legs are used, the body, always moist and somewhat slimy, being dragged passively along; and that for locomotion under pressure of unusual excitement the powerful body and tail muscles are brought into play. The body throughout its length is well marked off externally into segments, or metameres. One could not find an animal that combines the locomotor structures of both annelid and vertebrate better than does *Batrachoseps*.

There are twenty distinct segments between the girdles of these animals. Of the twenty-two specimens operated upon, the cord was severed between the fifth and sixth segments of some; between the tenth and eleventh of others; and of still others, between the fifteenth and sixteenth segments. In a few cases the section was made nearer the girdles, which always resulted in paralysis of the legs.

They usually recovered from the effects of the chloroform-ether mixture within five to fifteen minutes after taking it. The operation which consisted of simply snipping the spinal column in two with strong fine-pointed scissors, or destroying the nerve-cord by probing with a needle point, took only a minute or a minute and a half. Care was taken to injure as few of the muscles of the body-wall as possible and to avoid puncturing the peritoneum and the large blood-vessels, excepting in those cases where the animals were cut entirely in two.

In two specimens a piece of the spinal column about two mm. in length was removed. Shock effects occurred in only a few cases, which will be spoken of later on.

In all cases where the operation itself was successful and where the cord was not severed too near one or the other of the girdles coördinated movements were observed, not only between the members of the fore-legs and of the hind-legs, but also between the pairs themselves.

The animals operated upon were kept in broad flat-bottomed dishes. The floors of the dishes were kept covered with moistened layers of filter paper. During resting periods the animals were protected from the light of the room by being covered with fresh leaves or moist filter paper, and by covering over the dishes with towels.

When these coverings were removed the animals, usually asleep at the time, would sooner or later become aware that they were out in the open. They would then become restless. In their efforts to get under cover again one could note very easily the manner of their progress. Movements were usually initiated by the anterior parts turning to the one side and then to the other several times and finally back to the tail, often moving across it and twisting the body into a loop. During these movements the posterior parts would lie motionless and apparently helpless. After a number of these attempts at progressive locomotion the animal would start out straight ahead. The hind parts being unresponsive, it would tug and pull with the fore-legs in an effort to drag the helpless part along, and, in spite of the great length of the body and tail, and the extreme delicateness of the legs, the animal often succeeding in doing this.

The results of this tugging and dragging of the hind parts, while always the same, may be obtained by various methods, and were observed in my experiments as follows:

(*a*) Sometimes when the animals struck out in a forward direction and began to tug at the hind parts the hind-legs would begin to assist *before they were dragged in the least.* Their movements while slower than the fore-legs *coöperated toward forward locomotion*, and, furthermore, *were flexed and extended alternately*, that is, *they took forward steps alternately.*

(*b*) At other times no movements occurred in the hind-legs until the hind parts had been dragged along for a distance. The legs would then begin coördinate movements as described above. Sometimes the legs happened to be extended back along the sides of the tail and held up (surface tension of water and mucus alone being sufficient to support the weight of the legs) so that the toes did not touch the ground-surfaces. In such cases it was noticed that the hind-legs remained irresponsive for a longer time

than if they had been pendent enough so that the toes also touched and dragged along the ground.

(*c*) Coöperation on the part of the hind-legs could be started by touching with a pencil-point the skin of the sides of the body posterior to the section in the cord, or by touching the toes or the heels.

(*d*) A number of specimens would walk perfectly normally on their hind-legs when the front part of the body was held up and carried forward slowly. The walking movements would begin sometimes at once without dragging, sometimes after the hind-legs were dragged for a distance.

Experiments were made cutting *Batrachoseps* entirely in two as Friedländer had done with earthworms. The section was made at various levels between the girdles. Nothing but simple reflexes were obtained from the posterior halves although the pieces lived for days. The anterior halves, however, seemed to suffer no depression whatever. As soon as they recovered from the effects of the anæsthetic, they moved about in a manner that, with the exception of the awkwardness produced by the absence of the customary weight and resistance of the postetior parts and of the exhaltation produced by the operation, was perfectly normal. One of these anterior pieces lived for twenty-four hours. An hour before it died it was still breathing and moving about normally.

These results are about what one would expect to find in *Batrachoseps*. For, unlike earthworms, they cannot depend alone on the skin for respiration or upon an uncertain circulation. After sectioning the body the posterior half is deprived entirely of the benefits of the pharyngeal breathing and of the heart-beat, which continue on in the anterior half uninterrupted. After cutting an earthworm in two, respiration and the circulation can go on in the posterior half as well as they do in the anterior half. Hence the nervous responses in the one half are not different from what they are in the other half.[1]

5. *Summary and Conclusions.* — The results of the foregoing experiments on *Batrachoseps* may be summed up, and conclusions may be drawn, as follows :

[1] Friedländer, *loc. cit.*, p. 190.

(*a*) The coördinating center of locomotion in the hind-legs is located between the sixteenth and the eighteenth segments of the trunk.

(*b*) Walking movements in the hind legs after the spinal-cord is severed are due primarily not to impulses arising in the spinal centers, but to impulses that arise in the sensory cells of the periphery.

(*c*) These sensory impulses may be produced in the skin and muscles of the body-walls by stretching-stimuli; in the skin of the body-walls and of the legs by mechanical-impact-stimuli (friction- or tapping-stimuli).

(*d*) The fact that *Batrachoseps* with sectioned cords walk on their hind-legs when carried along by their fore-legs supports Loeb's idea that the same thing would obtain in dogs with sectioned cords if they could only stand up, or if their legs were shorter so that they might be effective in their movements when the trunk is prostrate. The difficulty in the dog is not due to the absence of the walking apparatus, but to the absence of "tone" in the muscles.

(*e*) Perhaps the essential thing supplied by the nerve-cord, as such, to the limbs during locomotion is this tone, this complimentary resistance of the muscles toward each other which keeps them ready for instantaneous regulated action, and which is probably maintained by impulses passing down from the organs or centers of equilibrium.

(*f*) If respiration could be properly maintained in the posterior half of *Batrachoseps* after being severed entirely from the anterior half, it is probable that walking movements could be started in the hind-legs by stretching-, or friction-, or tapping-stimuli, that is, by tugging gently at the front end of the posterior half, or by dragging it a distance over moist blotting paper, or by fastening it by means of a string to the anterior half and allowing the latter (which can walk along spontaneously) to pull at, or drag, the former along.

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